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Deterioration of Aspen clones in the middle Rocky Mountains

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DETERIORATION OF ASPEN CLONES IN THE MIDDLE ROCKY MOUNTAINS

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ABSTRACT

The frequent failure of deteriorating aspen (*Populus tremuloides* Michx.) clones to regenerate vegetatively by root suckers was studied by comparing the suckering capacity of these clones with adjacent healthy clones. Sucker production from root cuttings was used to evaluate the suckering capacity of a clone. Scarcity of regeneration in deteriorating clones was found to be unrelated to the ability of roots to sucker. A hypothesis based on the apical dominance phenomenon is presented to account for the low numbers of suckers produced by deteriorating clones. Stand data, sucker densities, and root ages of the clones are compared. Aspects of aspen deterioration discussed include relationship between deterioration and genotype, role of pathogens including viruses, and possibilities of revitalizing deteriorating clones by cultural methods.

INTRODUCTION

Before development of a fire suppression program in the Intermountain region, wildfires played an important role in the ecology of aspen (*Populus tremuloides* Michx.) (Loope and Gruell 1973). Frequent fires perpetuated the species because aspen is especially adapted to reproducing itself after its aboveground parts have been killed. Stands are regenerated vegetatively by adventitious shoots (suckers, or ramets) that originate irregularly on living roots. As a result of successive generations of shoots arising from a continually expanding root system, aspen occurs in large clones of genetically identical individuals (Barnes 1966).

When fire and other major disturbances are excluded from the environment, the ramets of a clone become mature in 80 to 100 years and then show a rapid decline in vigor and increasing susceptibility to disease and insects with advancing age.

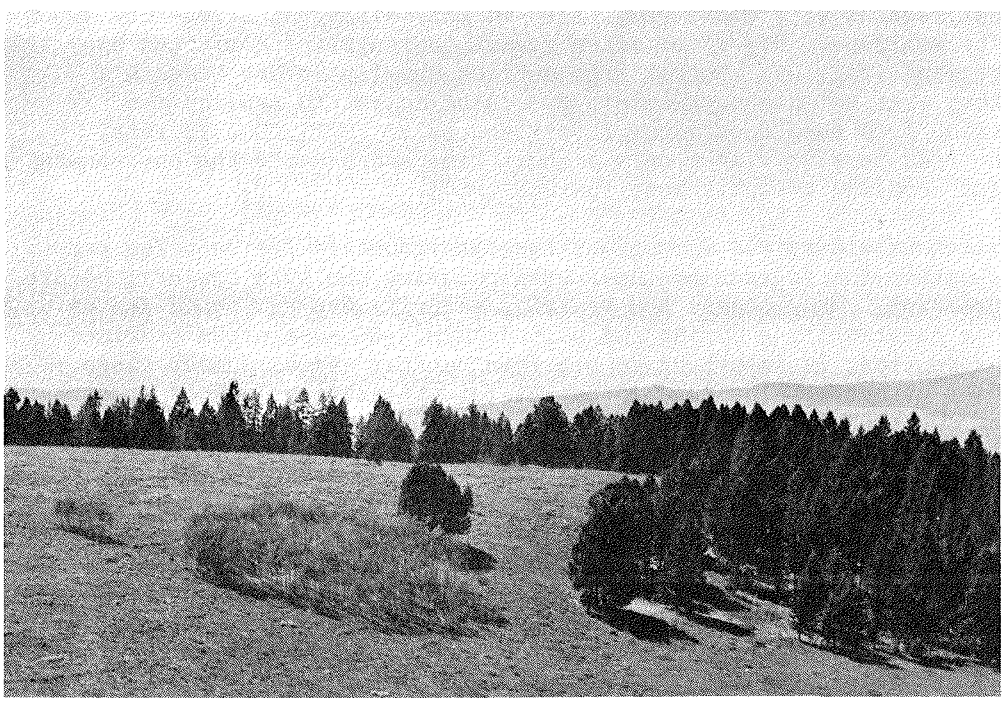
Deterioration is first evidenced by permanent openings in the canopy created by the death of individual stems. In a relatively short time, a scattering of diseased stems will be all that remains of a clone (fig. 1). On many sites, deteriorating aspen clones are replaced by conifers. Dry sites often revert to rangeland dominated by shrubs, forbs, and grasses (fig. 2). Sucker reproduction usually occurs beneath a deteriorating overstory, but often shoot numbers are insufficient to replace the mortality. Reproduction from seed does occur (Every and Weins 1971), but is rare, primarily because the seed remains viable only a short time and because the environment is usually too dry for seedling establishment (Barnes 1966).

Aspen deterioration is widespread throughout the Intermountain region. The ramets of most aspen clones within the region had their origin during the 19th century, before successful fire suppression. Many clones are reaching maturity; so we should see an increase in the number deteriorating during the next decade. Because aspen provides valuable watershed protection, is important as big game habitat and as summer range for livestock, has many esthetic values and potential for utilization in wood products, its future is a major concern of the resource manager.

Although the general pattern of aspen deterioration has been described in eastern (Graham and others 1963; Fralish 1972) and in western (Krebill 1972; Loope and Gruell 1973; Gruell and Loope 1974) States, no one has adequately explained why the production of root suckers is often insufficient to replace overstory mortality in decadent aspen clones. The purpose of this study was (1) to investigate the capacity of overmature aspen to produce root suckers and (2) to develop a hypothesis that would account for the scarcity of regeneration in deteriorating clones compared to the usually abundant reproduction that follows logging or fire.

1946

Figure 1.--Photographic record of aspen deterioration on the Beaverhead National Forest, Montana. The 1946 photo shows overmature aspen with young aspen in the understory (lower right quarter). Nineteen years later, most of these aspen have disappeared. In contrast, the small and the large clone in the lower left quarter of both photos have thinned out but have maintained themselves.



1965

Figure 2.--An aspen clone in advanced stages of deterioration in the Gros Ventre drainage of the Teton National Forest, Wyoming. The clone once supported a continuous crown cover over several hectares. The site has reverted to rangeland dominated by shrubs, forbs, grasses, and decaying aspen remnants. Heavy browsing by elk hastened this transition.

METHODS

The suckering capacity of deteriorating aspen clones was studied by pairing each of five deteriorating clones with an adjacent "healthy" clone. The five pairs were selected in an area east of Logan Peak on the Wasatch National Forest in northern Utah. Clones were distinguished by sex, leaf, stem, branching, and phenological characteristics (Barnes 1969). Deteriorating clones were characterized by low densities of living ramets and large numbers of dead stems, indications that these clones once had a higher level of stocking. Sucker reproduction was scarce in the clones selected. Two additional criteria for selection were absence of conifers and low incidence of sucker injury caused by livestock and wildlife. These standards were chosen to avoid possible confounding effects of conifer competition or animal browsing on the results of the study.

A healthy clone was defined as one having a stem density at least 75 percent that of fully stocked clones of the same mean age on similar sites. Openings in the crown canopy caused by the death of less vigorous, slow-growing ramets were rapidly filled by faster-growing individuals; thus there were no signs of deterioration. Healthy clones were sought near decadent ones to reduce site differences to a minimum. The maximum distance between paired clones was 50 m.

Clone data were obtained from randomly located 0.01-ha circular plots. Two plots were established in the healthy clones, which were relatively uniform, and three to eight in the deteriorating clones, depending on clone size and variation in stem density. Diameter at breast height (d.b.h.) of all stems exceeding 2 cm was measured on each plot in a clone. Five dominant and codominant trees were randomly selected for age and height determinations.

To determine the amount of regeneration present in the clones, sucker reproduction (shoots less than 2 cm d.b.h.) was sampled on randomly located 10-m^2 circular plots. Plot number varied with clone size.

Sucker production from root cuttings was used to evaluate the suckering capacity of healthy and deteriorating clones. Roots for testing suckering capacity were collected during the last 2 weeks of August 1972; collections from both stands of a healthy-decadent pair were made on the same day. Roots in the upper 50 cm of soil were excavated at 15 or more locations in a clone in order to sample the range in microsites. After collection, 30 root segments (10 by 1 to 2 cm) were randomly selected from the roots of each clone, rinsed in tapwater, and planted horizontally 1.5 cm deep in moistened vermiculite. Six groups of five cuttings from each clone were randomized in two plastic trays (three groups from a clone in each tray). Trays were placed in a greenhouse (25° C day, 15° C night), and watered lightly each day. Forty-two days after the roots were planted, all suckers taller than 5 mm were recorded.

From the range of root diameters (1 to 2 cm) used to ascertain sucker propagation, 12 roots were randomly selected from each clone for determination of mean root age.

RESULTS

Figure 3 shows the healthy and deteriorating aspen clones used in this study; descriptions are in table 1. Basal area was used as a measure of stand density. Density of deteriorating clones ranged from 6 to 30 percent that of the healthy clones with which they were paired. Distribution of stems in deteriorating clones ranged from a scattering of single stems to small groups of stems of varying densities. Deteriorating clones were visually distinguishable from healthy clones. Their stems tended to be shorter, branchier, and to have poorer form than stems in healthy stands. The last two morphological characteristics are typically under strong genetic control in many tree species (personal communication, Dr. B. V. Barnes, University of Michigan, Ann Arbor).

As table 2 shows, number and frequency of sucker clumps were better indices of regeneration in the aspen clones than numbers of individual stems (Smith and others 1972). Suckers tended to arise in clusters along roots, forming clumps of 1 to 15 shoots. It would be unrealistic to expect more than one sucker in a clump to develop into a tree. Frequency of suckers is important in evaluating regeneration in deteriorating clones because suckers are not uniformly distributed. They tend to occur in the vicinity of residual stems where root density is high. Excavations during root collections indicated that living surface roots did not extend far into the open spaces between scattered stems. Dead roots were numerous indicating the root systems were regressing. Even if all suckers in the deteriorating clones escape mortality and develop into mature trees, only a few small areas have the potential for reaching full stocking.

Table 1.--*Description of the stands of healthy and deteriorating aspen clones. The measurements shown are mean values determined by sampling*

Pair	Elevation (m)	Healthy clones					Deteriorating clones				
		Stem age (yr)	D.b.h.[1] (cm)	Total height (m)	Stems[2] per ha	Basal area (m^2/ha)	Stem age (yr)	D.b.h. (cm)	Total height (m)	Stems per ha	Basal area (m^2/ha)
1	2,100	70	15.0	11.9	1,740	32.1	65	20.7	12.8	277	9.5
2	2,100	91	14.4	14.2	1,604	27.2	80	15.9	7.6	306	6.3
3	2,300	83	21.2	15.9	986	35.6	83	16.8	11.9	215	2.1
4	2,000	77	19.3	16.8	806	25.3	82	18.2	9.8	94	2.7
5	2,500	92	21.1	15.9	541	21.8	74	20.2	11.6	143	5.0

[1]Diameter at breast height, 1.37 m.
[2]D.b.h. 2 cm and larger.

Healthy Clones Deteriorating Clones

Pair 1

Pair 2

Pair 3

Pair 4

Pair 5

Figure 3.--Healthy and deteriorating aspen clones used in this study. Fall photos were used to emphasize number of stems.

Table 2.--*Density of sucker regeneration in healthy and deteriorating clones expressed in number of individual suckers and in number of sucker clumps*

Pair	Healthy clones			Deteriorating clones		
	Suckers[1/] per ha	Clumps[2/] per ha	Frequency (percent)	Suckers per ha	Clumps per ha	Frequency (percent)
1	7,200	2,400	80	820	640	50
2	3,500	1,900	50	1,010	640	65
3	2,300	1,500	30	1,090	690	60
4	6,200	3,800	70	520	400	40
5	7,100	2,200	50	395	270	40

1/ D.b.h. smaller than 2 cm.
2/ Maximum area covered by a clump did not exceed a circular area 20 cm in diameter.

Sucker regeneration in healthy clones was relatively high compared to that in deteriorating clones (table 2). As in the deteriorating clones, numbers of individual suckers gave an inflated estimate of sucker reproduction and frequency data indicated that regeneration was not uniformly distributed throughout the clone. More than 50 percent of the suckers were less than 10 cm in height. Incidence of shoot dieback among suckers was common in the healthy clones.

Results from testing suckering capacity of root cuttings collected from healthy and deteriorating clones (table 3) indicated no clear-cut relationship between deterioration and ability to sucker. Of the deteriorating clones tested, two produced significantly fewer suckers than their healthy counterparts and two produced about the same number; one produced significantly more suckers than the healthy clone with which it was paired.

Table 3.--*Mean number of suckers (>5mm) produced from root cuttings (10 by 1 to 2cm) from healthy and deteriorating aspen clones and mean age of roots used; suckers were counted after a 42-day propagation period*

Pair	Healthy clones		Deteriorating clones		Significant[1/] difference in suckering
	Suckers per cutting	Root age (yrs)	Suckers per cutting	Root age (yrs)	
1	10.8	21.6	1.6	14.2	**
2	11.9	16.7	2.7	15.4	**
3	9.5	24.4	14.4	16.2	N.S.
4	7.0	15.0	21.8	10.8	**
5	14.3	10.4	18.6	9.6	N.S.
Av.	10.7	17.6	11.8	13.2	

1/ Determined by "t" tests: N.S.--nonsignificant; **--significant at p = 0.01.

Mean age of roots in the 1- to 2-cm-diameter class are shown in table 3. Differences in suckering capacity between clones in a healthy-deteriorating clone pair did not appear to be related to root age. Mean ages of roots from deteriorating clones were lower than those from healthy clones. A "t" test for paired replicates indicated that age differences were significant at the 5 percent level.

Necrotic areas were found in the bark of many roots of the deteriorating clone of pair 2 (fig. 3). These would seriously impair sucker formation because adventitious shoots are initiated in the region of the cork cambium. The number and size of necrotic areas on roots appeared to increase with root diameter (that is, age); so it seemed likely that sucker numbers would be inversely related to diameter. This was found to be true. Cuttings 1 to 1.5 cm (average age, 12.9 years) in diameter produced 5.9 suckers per cutting while those 1.5 to 2.0 cm (average age, 18.0 years) in diameter produced 1.1. The healthy clone of the pair showed no significant difference in sucker production between the two size classes.

DISCUSSION

Scarcity of regeneration in the deteriorating aspen clones used in this study does not appear to be related to suckering capacity of the roots. Although greenhouse tests showed that roots of some deteriorating clones produce relatively few suckers compared to their healthy counterparts, roots of others produced about the same or significantly more suckers than the healthy clones. Therefore, we must look for reasons in addition to loss in suckering capacity to account for poor sucker reproduction in deteriorating aspen clones.

The following is a hypothesis developed by the author to explain why regeneration is generally unsuccessful in deteriorating aspen clones. It was developed from the results of this study and from a general knowledge of the physiological mechanisms controlling sucker development:

> In healthy and in deteriorating aspen clones, auxin produced in shoots is translocated downward into roots where it inhibits sucker formation, a phenomenon known as apical dominance (Farmer 1962; Eliasson 1971a, 1971b; Schier 1973b, in press; Steneker 1974). Interference with this auxin supply changes hormone balances in roots enabling other hormones and such growth promoters as cytokinins to initiate regenerative processes.
>
> When the diseased overmature stems in deteriorating clones weaken and die, the root system dies back because the amount of photosynthate channeled to the roots is decreased by reduction in crown area. Residual stems maintain auxin levels in the smaller root system; so sucker production continues to be generally inhibited.

Mortality finally reduces the density in deteriorating clones to a scattering of overmature stems. Rate of decline depends on site, genotype, presence of competing vegetation, and browsing intensity by big game and livestock. Reduced clone vigor predisposes stems and roots to attack by various pathogens. At some stage, disease and reduced levels of carbohydrate reserves affect the suckering capacity of roots. It is then problematical how long a clone will continue to survive. As long as some roots are present and adventitious shoots are initiated and can grow into larger stems, ramets will maintain a clone in a given area.

A few suckers arise in deteriorating clones as they do in healthy clones because of various disturbances (Schier 1973a). Damage to roots by livestock and wildlife, insect and disease attacks, and even subtle environmental changes cause localized shifts in the hormone balance between growth promoters and inhibitors in roots, which triggers sucker formation.

However, after suckers are formed they are not free to develop unimpeded. Sucker growth is likely to be suppressed to varying degrees by apical dominance of the overstory. Environmental conditions for sucker growth are most suitable in open deteriorating clones because enough solar radiation reaches the forest floor. In healthy clones, low light intensity represses sucker growth. In addition, the humid environment is suitable for dieback fungi that attack the succulent shoots of young suckers.

Others have suggested that the appearance of suckers under an aspen canopy is evidence against an apical dominance theory. The suggestion ignores the fact that inhibition is not absolute and can be modified by a number of environmental factors.

It was interesting that aging of roots in the 1- to 2-cm-diameter class, the size range used for sucker propagation, indicated that roots of deteriorating clones were significantly younger than those from healthy clones. Possibly, in a root system that is dying back, older, less vigorous roots would be the first to die, which would tend to lower the mean age of remaining roots.

It is not unusual, as in this study, to find a deteriorating clone adjacent to a healthy one, ramets of both probably having been established at about the same time. The close relationship between deterioration and clone characteristics suggests that genotype may be the controlling factor in the timing and rate of decline.

Aging, which is manifested by reduced growth, a decrease in metabolism, an increase in dead branches, and lower resistance to disease and insects, may occur at a more rapid rate in some genotypes than others. Clonal differences in susceptibility to pathogens (Mielke 1957; Wall 1971; Copony and Barnes 1974) and insects may also account for variation in clone condition. One would also expect clones with inherently poor suckering capacity to be less able to reproduce during deterioration than those with high suckering capacity.

There may even be genotypes in which apical control is weak or the level of growth-initiating factors is high so that stands sucker vigorously at the least disturbance (fig. 4). The uneven-aged ramets of many selected clones that Alder (1970) studied in Utah and northern Arizona indicate there are clones in which mortality is quickly replaced by adventitious shoots.

The abundant production of suckers that usually follows logging, fire, or any other major disturbance that kills all or most stems within a short time demonstrates

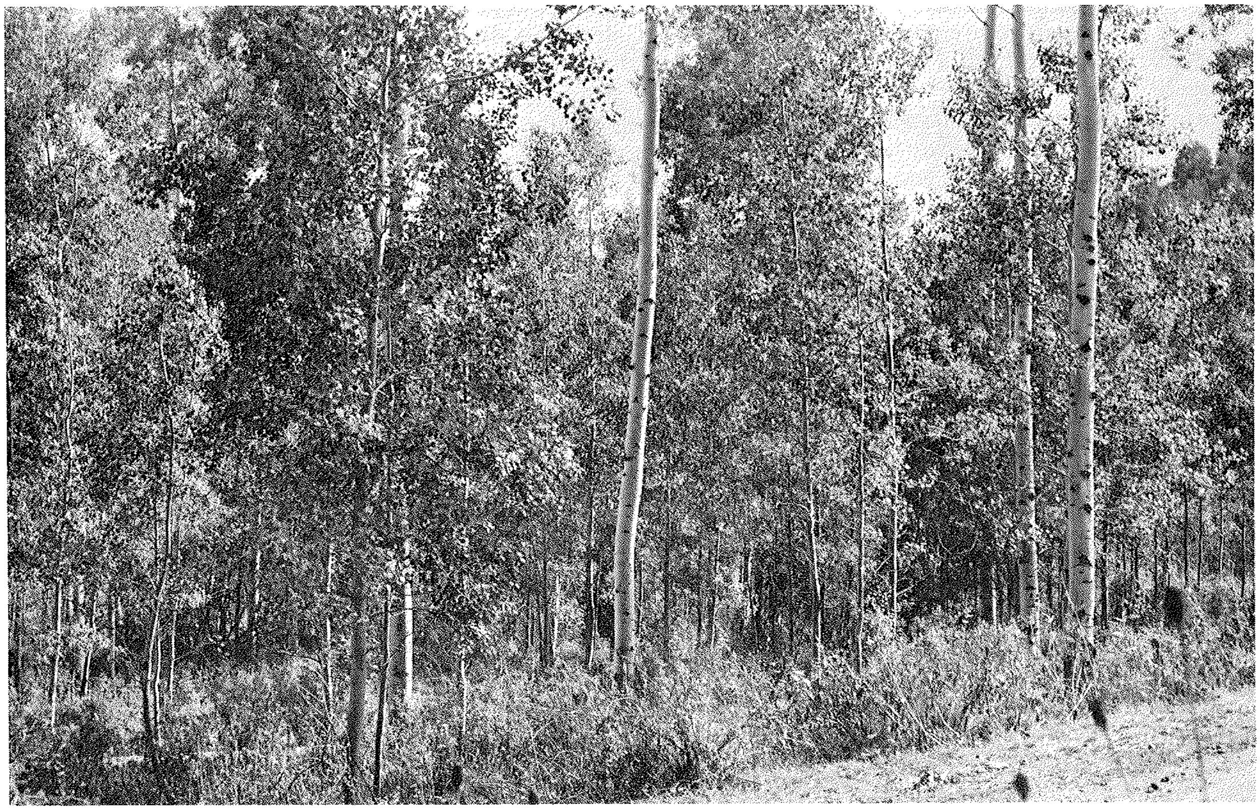


Figure 4.--The abundance of suckers in this understory of overmature ramets demonstrates that some clones sucker profusely during deterioration (Wasatch National Forest, Utah). There were no signs of a major disturbance that could have stimulated suckering. Ramets of this clone have good form and low branchiness. In contrast, the deteriorating clones used in this study have a ratty appearance (see fig. 3).

that regeneration is usually no problem when an aspen stand is wiped out relatively fast. The rapid death of stems eliminates apical dominance while the original root system can still produce suckers.

However, it is not unusual to find large numbers of suckers in the understory of diseased aspen. Pathogens may stimulate suckering by affecting auxin metabolism or transport. Stands attacked by aspen leaf blight (*Marssonina populi* [Lib.] Magn.), to which aspen shows a high clonal variation in susceptibility (Mielke 1957), often have well-established regeneration. Figure 5 shows the scattered remnants of an aspen clone (first observed by Tew [1967], his clone 1) after a series of attacks by *Marssonina* over about 10 years and the young stand that has become established in the understory. The blight does not appear to be causing mortality in the regeneration. Sprouting is vigorous beneath the thin overstory of mature aspen stands in Wyoming that are dying out in the presence of viruslike symptoms (personal communication, Dr. W. D. Ross, University of Wyoming, Laramie).

Insect outbreaks also cause the development of suckers in the understory of mature aspen. Defoliation of aspen in interior Alaska from 1965 to 1968 by the large aspen tortrix (*Choristoneura conflictana* Walker) resulted in suckering in some clones before the growth of new leaves (personal communication, Dr. J. C. Zasada, USDA Forest Service, Institute of Northern Forestry, Fairbanks, Alaska).

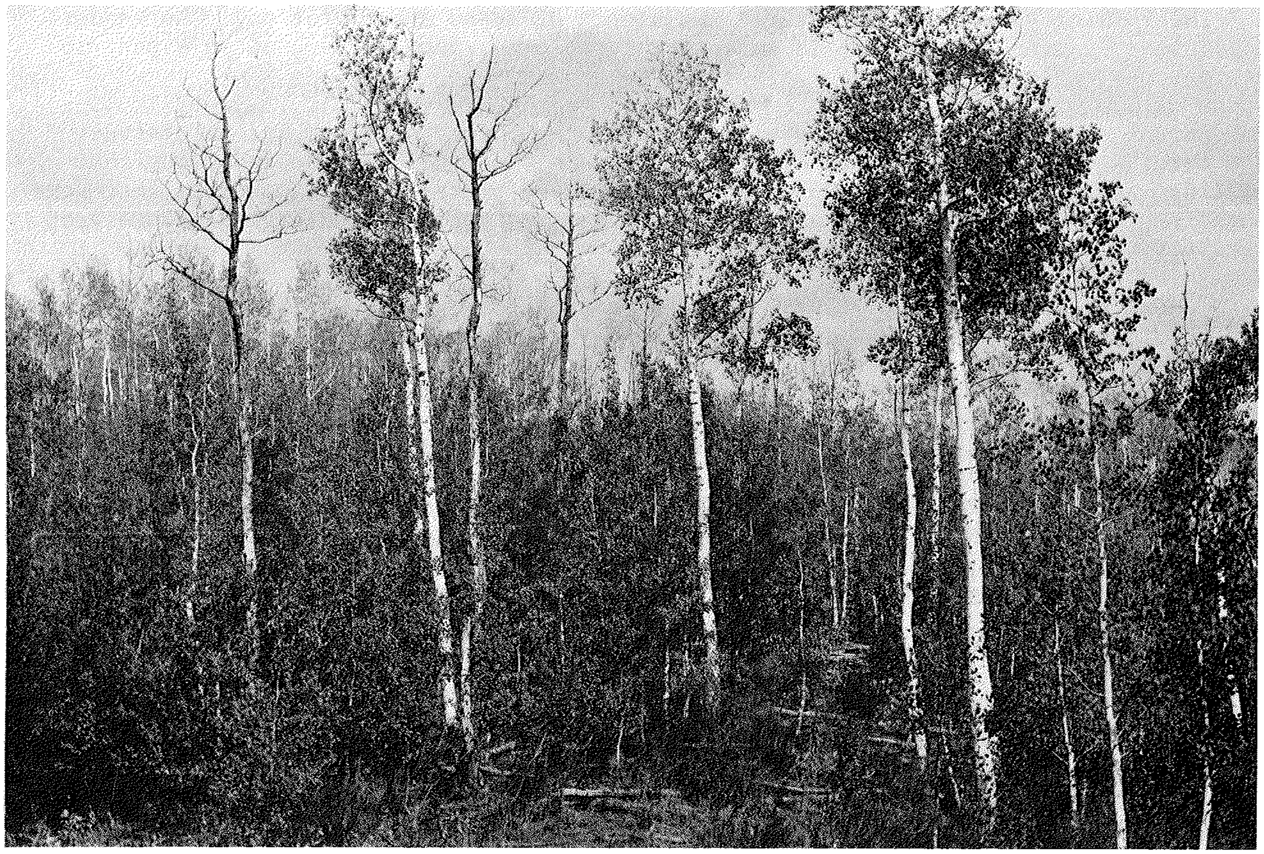


Figure 5.--Mortality has been heavy in this clone because of repeated attacks by Marssonina populi *(Wasatch National Forest, Utah). The actual cause of mortality may have been caused by a secondary pathogen that attacked weakened trees. The blight apparently has reduced the effects of apical dominance which has resulted in abundant sucker production.*

To revitalize a deteriorating aspen clone, treatment must stimulate suckering. Suckering can be promoted by killing stems in such various ways as by clearcutting, controlled burning, or herbicide spraying. Deteriorating clones probably vary in their potential for producing regeneration because of clonal variations in suckering capacity (Schier 1974), and differences in root density and site factors. When all that remain of a stand are a few scattered, widely spaced stems, the roots necessary for producing a uniformly dense stand of suckers are not present. Root density has probably declined to such an extent that, after the clone is treated, regeneration will consist of small groups of suckers in the vicinity of stumps or dead stems. In time, these groups may increase in size as roots grow into the intervening spaces and repeated generations (rotations) of raments are produced by periodic killing of stems.

Another regeneration problem could result from the effects of pathogens in residual trees. These may seriously reduce root suckering capacity and sucker growth.

Other important regeneration problems are caused by competing vegetation and browsing by livestock and wildlife. Heavy browsing on elk winter ranges can totally suppress regeneration and speed up succession by conifer types or shrub, grass, and forb communities (Krebill 1972; Gruell and Loope 1974). Often, however, when aspen fails to regenerate there is a tendency to blame livestock and wildlife without investigating. This paper has shown that physiological mechanisms inherent to the clonal growth habit of aspen can prevent sucker production.

The role of viruses is an interesting aspect of aspen deterioration. The reader should bear in mind that little is known about the occurrence of viruses in aspen; so this discussion is largely speculative.

An unknown factor in aspen deterioration is the effect of clone age as distinct from ramet ages. The large size of aspen clones in Utah and Colorado indicates that seedlings were established many years ago (Barnes, in press). It is possible that some clones may have been initiated during Pliocene or Miocene times, enlarging themselves asexually through many generations of ramets.

Generally, when a clone of any plant is propagated vegetatively for a long period of time, it becomes infected with one or more viruses (Hartmann and Kester 1968). The clones degenerate with age because plants apparently never free themselves from virus infections (Bowden 1964). Once infected, a plant remains so for as long as it lives. Further, when vegetative parts of that plant are used for propagation, the progeny will also be infected in perpetuity.

This persistence of viruses means that vegetatively propagated plants probably are continually affected by all the viruses they have ever contracted. Of all pathogens, viruses are the most likely to cause the degeneration of clones with age, but systemic infection by fungi and bacteria might also be important. Considering the length of time aspen has reproduced vegetatively, it would be surprising not to find clones infected with viruses and other pathogens. Damage caused by these pathogens might intensify and spread in overmature ramets of low vigor.

In addition to its role in aspen regeneration, fire may also have controlled viruses and other pathogens in aspen clones. Periodic destruction of diseased plants by burning probably reduced the amount of inoculation and thus slowed the rate at which pathogens were transferred to a new crop of suckers. Removal of stems in logging may accomplish similar results.

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